SPECIES CROSSES IN HELIANTHUS:
II. POLYPLOID SPECIES[1]

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Cytological studies of interspecific hybrids in *Helianthus* have, with few exceptions, shown that a high degree of interspecific chromosomal homology exists. The exceptions are of special interest in that they supply us with important clues concerning the interrelationships of species or groups of species. How important such clues may be in answering questions concerning the origin of the polyploid species is not yet clear,

The work of Kostoff (1939) on the hybrid *H. tuberosus* × *annuus* provides us with the first important cytogenetic study relating to the problems surrounding the origin of polyploid sunflowers. He discovered that this hybrid of a hexaploid perennial ($2n = 102$, *H. tuberosus*) and a diploid annual ($2n = 34$, *H. annuus*) often formed 34 bivalents in meiosis. He concluded that the chromosomes of *H. annuus* were essentially homologous with one genome of *H. tuberosus*, and that the remaining 17 bivalents resulted from autosyndesis of 2 sets of *H. tuberosus* chromosomes. This auto-allopolyploid interpretation of *H. tuberosus* has remained essentially unchallenged although Darlington (1956) implies that it is an autoploid of *H. annuus*.

Several interesting questions are posed by Kostoff's work. (1) Is the genomic composition of *H. tuberosus* unique for the genus or are other hexaploid species similarly constituted? (2) Is there additional evidence for the existence of A and B genomes in *Helianthus*, and if so, what is the source of the B genome in *H. tuberosus?* Some of the information accumulated by us on crossing relationships and cytology in *Helianthus* bears directly on these problems. The pertinent observations are these: (1) annual sunflowers (all of which are diploid) probably possess the same basic genome (B

genome of Kostoff), but the individual species have undergone considerable chromosomal differentiation through reciprocal translocation (Heiser 1961). (2) Most diploid perennial sunflowers show exceedingly close chromosomal constitutions among themselves, but their genome differs from the "annual" genome (Heiser, Martin and Smith 1962), (3) tetraploid sunflowers (all perennials) are either autoploid or are segmental allopolyploids based on the "perennial" genome (A genome of Kostoff) (Smith 1961), (4) hybrids between *H. annuus* (diploid) and *H. decapetalus* (tetraploid) typically produce 17 bivalents and 17 univalents during meiosis (Heiser and Smith 1960), this being interpreted as a case of autosyndesis of the *H. decapetalus* chromosomes and asynapsis of the *H. annuus* chromosomes. Although no absolute proof can be given that the asynaptic chromosomes are indeed those of *H. annuus*, circumstantial evidence strongly supports this conclusion. (5) Clevenger and Heiser (1963) have shown that *H. tuberosus* crosses readily with *H. rigidus*, and that meiosis in these hybrids is essentially the same as in the parental species. Therefore, *H. rigidus* is genomically similar to *H. tuberosus*.

This paper is a presentation of the results of additional studies of hybridization involving polyploid sunflowers and a discussion of these results in terms of the genomic constitution and origin of the polyploid species of the genus and their relationships to the taxonomic complexities of the genus.

MATERIALS AND METHODS

Plants used in this study were usually obtained from wild populations and were propagated from seeds or as clonal transplants in experimental gardens and greenhouses. Voucher specimens are preserved in the Indiana University Herbarium. Cytological observations were made on microsporocytes prepared by the acetocarmine squash technique. Estimates of fertility were based upon the stainability of pollen grains in aniline blue in lacto-phenol. Chromosome doubling was obtained either by applying a few drops of .2% solution of colchicine by eyedropper to vegetative buds over a period of days or by growing young seedlings

for 8 hours on filter paper saturated with a .2% solution of colchicine. Although only a small number of polyploids was secured by either method, the treatment of seedlings proved the more successful.

TETRAPLOIDS

Five of the six species known to include tetraploids ($n = 34$) are distributed in eastern and central North America, and their similar morphology as well as the results of cytogenetic studies indicate that they are closely related (Fig. 1). The sixth, *H. ciliaris*, occurring in the southwestern United States and northern Mexico, is significantly different in gross morphology, and has not been successfully hybridized with the other tetraploid sunflowers.

The hybrids *H. decapetalus* × *strumosus* and *H. strumosus* × *hirsutus* have been described previously (Smith, 1961). The following additional hybrids may now be reported.

H. decapetalus × *laevigatus* and reciprocal (H476a + b). Four of the F_1 hybrids showed over 90% pollen stainability and the fifth gave a count of 43%. Seed set was good in all the plants. Meiotic chromosome behavior was examined in two of the plants and was not significantly different from that observed in the parents. Many cells showed 34 pairs, but occasional cells were observed in which one or two quadrivalents were present. An F_2 family (H655) of 21 plants was grown. Five of the plants died, four were extremely weak, but the remainder were vigorous. Pollen stainability ranged from 30 to 99% with a mean of 66%.

H. hirsutus × *smithii*[2] (H572b). Five hybrids were ob-

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[2]**Helianthus smithii**, Heiser, *nom. nov.*, *H. parviflorus* var. *attenuatus* A. Gray Syn. Fl. N. Am. 12: 278. 1884. (T.: Georgia, Rabun Co., near Talullah Falls, *J. Donnell Smith 6* (GH!). Alab. Randolph Co., 3 mi. n. of Wedowee, *D. M. Smith 1482*, K44 (IND). *Helianthus parviflorus* Bernh. is a synonym of *H. microcephalus* Torrey and Gray, and the name *H. attenuatus* is already occupied. Thus, it is necessary to supply a new name for this species. Its affinities apparently are with *H. strumosus* rather than with *H. microcephalus*. Since two Smiths have been concerned with making this sunflower known, this particular specific epithet seems most appropriate. — C. B. H.

Fig. 1-6. Camera lucida drawings of meiotic chromosomes in *Helianthus*, × approx. 950.

Fig. 1. *H. hirsutus* × *decapetalus* (6224), 34_{II}.

Fig. 2. Colchicine induced tetraploid of *H. microcephalus* × *giganteus* (C6371), $32_{II}1_{IV}$.

Fig. 3. *H. resinosus* × *tuberosus* (P130a), $49_{II}1_{IV}$.

Fig. 4. Colchicine induced tetraploid of *H. decapetalus* (P412c), $28_{II}3_{IV}$.

Fig. 5. *H. strumosus* × *annuus* (H626c), $17_{II}17_{I}$.

Fig. 6. *H. schweinitzii* × *smithii* (H474b), $34_{II}17_{I}$.

Overlapping chromosomes in fig. 3-6 have been moved in drawing.

tained from this cross and were fertile, with pollen stainability ranging from 80 to 99%, with a mean of 92% and good seed set. Meiosis was of the typical tetraploid sunflower pattern, with one or two quadrivalents, and with the remaining chromosomes forming bivalents.

Hybrids have also been obtained between *H. smithii* and *decapetalus* (H571a), and *H. smithii* and *strumosus* (6250). These plants showed 87% or better pollen stainability. They were not analyzed cytologically.

Colchicine-induced tetraploids have been obtained from three perennial hybrids and one perennial species. The tetraploids of hybrid origin *(H. giganteus × microcephalus* 325076, 1 plant; *H. microcephalus × giganteus* C6370, 2 plants; and *H. maximiliani × 2n decapetalus,* C6371, 2 plants) were essentially similar morphologically to the diploid hybrids from which they were derived except for slightly larger heads. All of them showed over 90% pollen stainability, although seed set was somewhat reduced. Meiosis was also essentially similar in all five of the plants with one to three quadrivalents being observed in most cells (Fig. 2) and an occasional cell showing 34 pairs. The one successful doubling of a diploid species involved *H. decapetalus* (P412c). In 28 cells studied at diakinesis from one to five quadrivalents were observed with the remainder of the chromosomes associated as bivalents. The most frequently observed configuration was 28_{II} and 3_{IV} (Fig. 4). Unfortunately the plant was lost before fertility was determined.

One other hybrid has been obtained that bears on the origin of the tetraploids. This cross involved *H. hirsutus* as the female parent and a diploid form of *H. decapetalus* (6224). This plant, however, was tetraploid rather than the expected triploid. Since it was morphologically more or less intermediate between the parents it seems likely that it is a hybrid involving an unreduced gamete of the diploid parent. The plant showed 93% pollen stainability and 34 pairs in each of the seven cells examined.

HEXAPLOIDS

Seven taxa which are regarded as species are hexaploid

($2n = 102$), although two of these also include tetraploid races *(H. ciliaris, H. strumosus)*. If Watson's (1929) treatment of the genus were to be followed, many more hexaploid species would be recognized. However, his additional taxa are very difficult to justify even on morphological grounds, and when other biological criteria are considered, their justification becomes even more difficult. Two of the species under consideration here, *H. strumosus* and *H. tuberosus*, are widespread in eastern North America, and *H. rigidus* is a common species of the mid-continent region, its range overlapping the ranges of the two preceding species over a large area. The two western American species, *H. ciliaris* and *H. californicus*, have not been hybridized with the other hexaploids even though several attempts have been made. The two remaining species are restricted to the southeastern United States, *H. schweinitzii* occurring in only a few localities in North Carolina, and *H. resinosus*[3] being widespread in the Southeast, but not common. The five eastern hexaploids have now been connected by a series of crosses.

The following hybrid combinations have been successful: *H. resinosus* × *schweinitzii* (H451a+b), *H. resinosus* × *strumosus* (H475a+b, K70a+b, K130, K199, K200), *H. resinosus* × *tuberosus* (P130a+b), *H. rigidus* × *strumosus* (H457a), *H. rigidus* × *tuberosus* (see Clevenger & Heiser, 1963), *H. schweinitzii* × *tuberosus* (K88a, K138 a+b), *H. strumosus* × *tuberosus* (P176a+b). Reciprocal hybrids were obtained in every case except *H. rigidus* × *strumosus*, in which seed germination failed in the reciprocal cross. The results of hybridization were so similar in each case that they need not be discussed separately. The F$_1$ generation

[3]This name is being used to replace *H. tomentosus* of authors. Jones and Fuller (1955) were apparently the first to note the misapplication of the name *H. tomentosus* Michx. by American authors. We agree that Michaux was referring to an Illinois plant (although we have not seen the type) but disagree that extant Illinois plants should be called *H. tomentosus*. The material so designated by Jones and Fuller (1955) and Jones (1963) is well within the range of our concept of *H. tuberosus*. The next available name for the hexaploid southeastern sunflower in question is *H. resinosus* Small, Fl. S. E. U. S., p. 1269 1903. (T.: Fla., Gadsden Co., *Nash 2581.* NY!).

was highly fertile (85-100% stainable pollen) and vigorous, and essentially intermediate between the two parents in gross morphology, with the exception of certain features in the hybrid of *H. schweinitzii* × *tuberosus*. The parents of this hybrid differ strikingly in the nature of their underground perennating organs; *H. schweinitzii* has diffuse fleshy roots with new growth arising either directly from these or from the stem base, while *H. tuberosus* has long rhizomes which terminate in fleshy tubers, the latter constituting the source of the next season's growth. The hybrid has both fleshy roots *and* short tuber-bearing rhizomes. The study of meiosis in hexaploid sunflowers is difficult, but all available evidence suggests that the F_1 hybrids do not differ significantly from their parents in meiotic behavior. Meiosis is somewhat irregular in that multivalents are encountered in most cells (Fig. 3). The number of multivalents (probably quadrivalents) ranges from 1 to 4, with the other chromosomes forming bivalents.

A few small backcross and F_2 families of several combinations have been grown which showed a wide range of morphological expression, but little weakness or sterility was encountered.

Many crosses have been attempted between plants of different ploidy level. These may be grouped into the following three categories:

1.   4N PERENNIALS × ANNUALS. The following triploid hybrids have been secured: *H. decapetalus* × *annuus* (P338, H626), *H. decapetalus* × *debilis* ssp. *cucumerifolius* (H645d, DCDI), *H. decapetalus* × *debilis* ssp. *hirtus* (H649, H650), *H. hirsutus* × *annuus* (P339, H628), *H. hirsutus* × *debilis* ssp. *cucumerifolius* (H647), *H. strumosus* × *annuus* (P337, H626C).

These hybrids are rather difficult to secure and generally are more readily obtained with the tetraploid as the female parent. Vigorous triploids have been obtained in all combinations but weak and malformed plants are not uncommon. With the exception of the hybrid between *H. strumosus* and *H. annuus* all of the plants were winter killed when grown

out of doors but behaved as perennials in the greenhouse. Pollen fertility is usually quite low (1-15%) but one hybrid of *H. hirsutus* × *debilis* ssp. *cucumerifolius* gave a count of 64%. Most heads are absolutely barren. At meiosis the most commonly observed configuration is 17 pairs and 17 univalents (fig. 5) but considerable variation is encountered similar to that previously reported for *H. decapetalus* × *annuus* (Heiser and Smith 1960). Morphologically, the plants appear more nearly like the tetraploid parent but some influence of the annual parent can be detected. Triploid plants were treated with colchicine in two different years but no chromosome doubling occurred.

2.   6N PERENNIALS × ANNUALS.   The only hybrid we have of this combination is between *H. tuberosus* × *annuus*. We have made this hybrid using two strains of *H. tuberosus* and four of *H. annuus* (H633Q, R, T, and S). Pollen stainability varies from 12 to 53% and the plants are mostly seed-sterile although an occasional filled achene is produced. The plants are all vigorous and overwinter in the field at Bloomington.

This hybrid has received considerable attention in Europe as a potential economic plant (Rudorf 1958) and the hybrid has been analyzed cytologically by Kostoff (1939). Our material has been unfavorable for detailed cytological study but we have made some studies of another hybrid (P194) supplied to us by the United States Department of Agriculture. In 20 cells studied a mean of 31 bivalents was found with the remainder of the chromosomes appearing as univalents or multivalents. These results agree fairly well with those of Kostoff. However, he observed bridges and fragments in his hybrid and in 50 cells of our material only a single bridge was seen at anaphase.

Other crosses involving an annual and a hexaploid species have been described by Wagner (1932) but he did not include cytological analyses and the identification of the parents of his hybrids is open to question.

3. PERENNIALS × PERENNIALS. Although several attempts

have been made by us, Long (1955), and Jackson (unpubl.) to secure crosses of diploid perennials with both the tetraploid and hexaploid species, no hybrids have been secured.

Various crosses between tetraploid and hexaploid species have been obtained, however. The initial cross gives very few seeds, but the resulting offspring are extremely vigorous. The hybrids secured and their fertility are as follows:

H. hirsutus 4n × *tuberosus* 6n (H452). 3 plants; pollen stainability 34 to 40%; seed set 10 to 20%.

H. smithii 4n × *strumosus* 6n (H570a + b). 8 plants; pollen stainability 83 to 99%; seed set 10 to 25%.

H. resinosus 6n × *decapetalus* 4n (H495). 1 plant; pollen stainability 62%; no seed set.

H. schweinitzii 6n × *smithii* 4n (H474b). 1 plant; pollen stainability 75%; seed set not known.

H. resinosus 6n × *smithii* 4n (K127b). 1 plant; pollen stainability 79%; no seed set.

H. decapetalus 4n × *resinosus* 6n (K183-5). 1 plant; no stainable pollen; no seed set.

Meiosis was examined in one or two plants of each combination. The number of pairs ranged from 31 to 34 with the remainder of the chromosomes appearing as univalents; 34 pairs and 17 univalents (Fig. 6) were observed in several cells.

ONE GENOME OR TWO?

Following Kostoff (1939) we have regarded *Helianthus* as having two distinct genomes. Our earlier work (1962) tended to support this assumption. Hybrids between diploid perennials and annuals are extremely difficult to secure and those that have been secured have been highly sterile and showed a highly irregular meiosis. In the hybrid, *H. canus* × *angustifolius*, several univalents were always observed and in the hybrid *H. debilis* × *floridanus* pairing was extremely variable although 17 pairs were observed in two cells (Heiser, Martin and Smith 1962). Recently hybrids have been secured between *H. niveus*, a member of the annual assemblage, and the perennials, *H. microcephalus*,
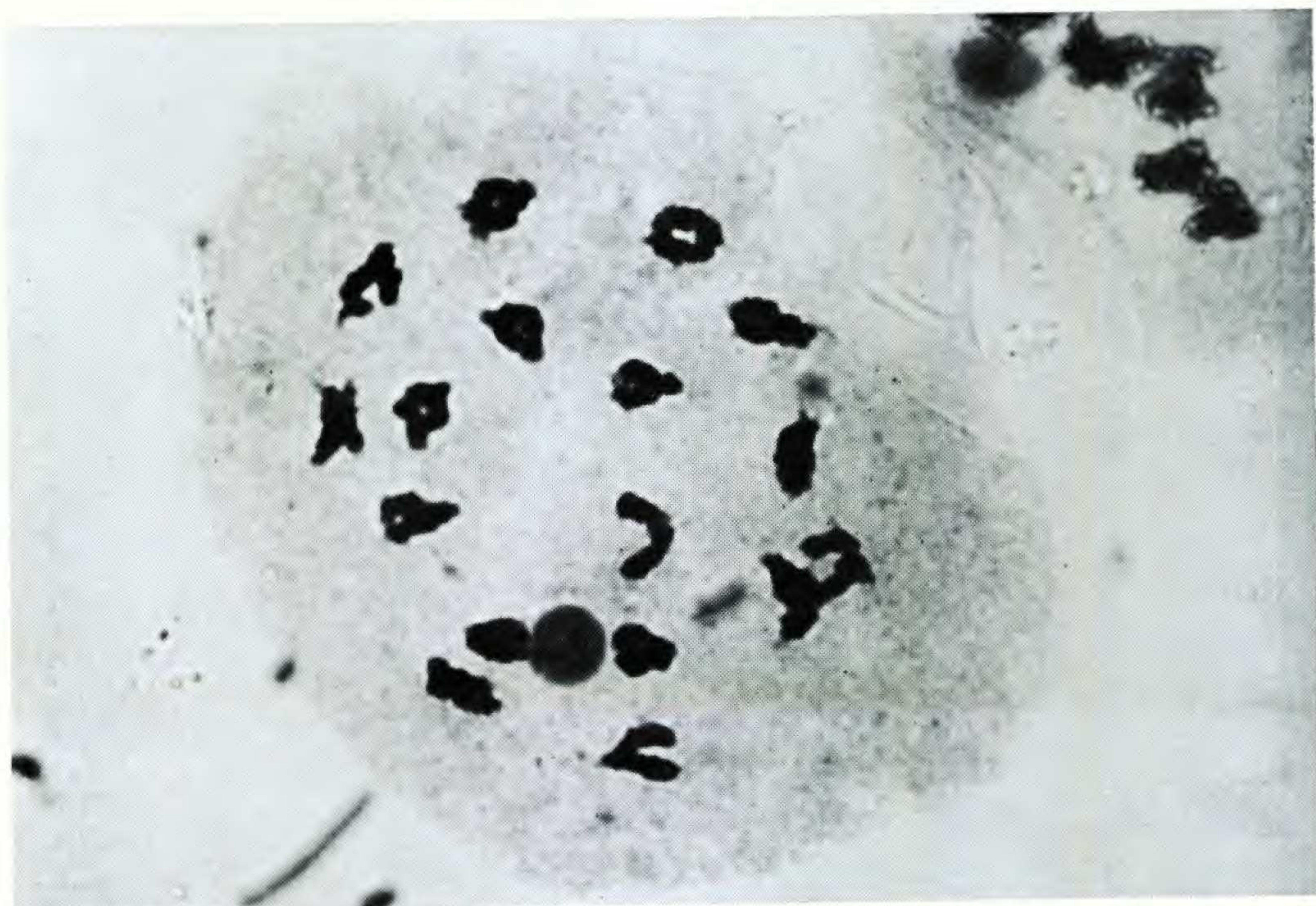
Fig. 7. Photograph of meiotic chromosomes in *Helianthus debilis* ×
occidentalis (H651), 17_{II}, × approx. 1300. Fig 7 is plate 1306.

H. nuttallii, and *H. occidentalis*, which although highly sterile
(0-12% stainable pollen, and no seed set) show from 14 to
17 pairs at diakinesis. In the two hybrids secured between
H. debilis and *H. occidentalis*, both highly sterile, one plant
showed 17_{II} (Fig. 7) in 20 cells whereas the second plant
had a highly irregular meiosis that did not lend itself to
detailed analysis.

If, as we are assuming, the pairing in these annual-per-
ennial hybrids is allosyndetic, and if one regards failure of
pairing to be essential to the recognition of named genomes,
then it indicates that we can not regard *Helianthus* as having
distinct genomes. On the other hand, in view of the con-
siderable genetic differentiation between the annual and
perennial sunflowers and the sterility in the F_1 hybrids it
might be desirable to continue to speak of A and B genomes
in *Helianthus*

DISCUSSION

The data presented here and those published previously
on hybridization in *Helianthus*, provide the basis for some

tentative conclusions about the interrelationships and proba-
ble mode of origin of the eastern North American polyploid
species of the genus. It is doubtful that the cytogenetic
study of other hybrid combinations will yield much more
data than we now have because of the physical limitations
imposed by the large number of chromosomes and the pos-
sibility of pairing between the chromosomes of the annual
and perennial species. Other approaches, such as the use
of chromosome morphology and chromatography (Smith &
Levin, 1963), are definitely in order, but since such new
studies may not yield relevant information for some time,
it seems desirable to present our tentative conclusions about
this group of sunflowers,

ORIGIN OF TETRAPLOIDS. It seems highly probable that the
tetraploid species arose from eastern perennial diploids
through allopolyploidy. The possibility that one of them,
H. decapetalus, is an autopolyploid exists, although it may
well be an allopolyploid (Smith 1960). Morphologically, the
tetraploid perennials are very similar to many of the diploid
perennials, for example *H. hirsutus* to *H. divaricatus*.
Moreover, the few experimentally induced tetraploids show
pairing very similar to that of naturally occurring tetra-
ploids, and an apparently unreduced gamete of *H. deca-
petalus* functioned to produce a fertile tetraploid hybrid
with *H. hirsutus*. Since it was shown in the previous paper
of this series (Heiser *et al*, 1962) that the diploid hybrids
display good chromosome pairing, the tetraploid species
derived from them would be classed as segmental allopoly-
ploids, following the classification of Stebbins (1950).

ORIGIN OF THE HEXAPLOIDS. On the basis of the chromo-
some pairing relations in the hybrid *H. tuberosus* × *annuus*,
Kostoff (1939) suggested a genomic formula of $A_t^1 A_t^1 A_t^2$-
$A_t^2 B_t B_t$ for *H. tuberosus* and postulated that the B_t genome
was similar to that of *H. annuus*. Since all the eastern
hexaploid perennials give largely fertile hybrids with fairly
good chromosome pairing it seems possible that all of them
may have a similar genomic make-up. There can be little
doubt that two genomes (the A genomes of Kostoff) of the

hexaploids come from the tetraploid perennials. This is suggested not only in the results secured from the crossing of tetraploids and hexaploids but also on morphological grounds; *Helianthus strumosus*, for example, exists as both a tetraploid and a hexaploid.

Our problem then concerns the source of the third genome (the B genome of Kostoff). Our data from the analysis of triploids in which we frequently find 17 pairs and 17 univalents might be used to support Kostoff's claim if we postulate pairing of the perennial genomes and univalent formation from the annual genome. Such hybrids, if doubled, would produce hexaploids. On the basis of their present distribution it seems unlikely, however, that any of the annual species could represent one of the progenitors. *Helianthus annuus* is the only species that is sympatric with the majority of the tetraploids and hexaploids and it is probable that it was introduced into the eastern United States in recent times by man (Heiser 1955). If an annual genome is represented we would have to postulate that its combination with the A genome must have occurred at some time when the distributions of the species were quite different from that seen today.

Morphologically, our studies thus far have shown no indication of the annual sunflowers in the hexaploid species, with the possible exception of the large size of certain characters in cultivated forms of *H. tuberosus*, and it is quite possible that this increased size could have come about through artificial selection by man. Although we might expect that the two genomes of perennial sunflowers might effectively mask any feature supplied by the annual genomes, it must be admitted that the influence of the annual can be detected in the triploids. However, the very fact that triploid hybrids can be secured between perennials and annuals, whereas perennial diploid × tetraploid hybrids have not been secured, may be significant. So far, however, it has been impossible to secure doubling in any of the triploids.

The possibility that the hexaploids may have had their origin entirely from the eastern perennials, which would be

more reasonable in light of the present geographical distribution of the species concerned, deserves serious consideration. It has already been pointed out that this could be justified on morphological grounds. The 34 pairs and 17 univalents resulting in the crosses between the hexaploid and tetraploid perennials also do not rule out this possibility. If the parental gametes were $A_1A_2A_3$ and A_1A_2 — where the subscripts represent genomes of different diploid perennials — we might expect such pairing rather than the formation of trivalents. The pairing observed in the *H. tuberosus* × *annuus* plant also would not necessarily negate this hypothesis. If, for example, *H. tuberosus* is $A_1A_2A_3$ or perhaps $A_1A_1A_3$ we might expect pairing of A_1 with A_2 or A_1 with A_1 and pairing of A_3 with the B genome of *H. annuus*. Here again critical crosses that would give evidence of this have not been secured. However, in the diploid perennial × diploid annual hybrids now known, up to 17 bivalents are not uncommon, indicating that pairing can occur between the chromosomes of the annuals and perennials.

Although some evidence on the origin of the hexaploids might be provided by securing hybrids between diploid and tetraploid perennials, it seems unlikely that genomic analysis can provide critical evidence on the origin of the hexaploids. The question of the origin of the third genome therefore must remain open until additional lines of investigation are pursued.

TAXONOMIC SIGNIFICANCE. The bearing of polyploidy on the species problem has already been discussed for the tetraploids (Smith 1961) and these remarks apply equally well to the hexaploids. It is the polyploid species that have given the genus the reputation of being taxonomically difficult. The diploid species, in spite of rather extensive inter-specific hybridization, offer far fewer taxonomic problems. Whether one species, a few species, or many species are recognized in the polyploids is largely a matter of personal choice. We follow the second course and in so doing reflect the opinions of most taxonomists, excepting Watson (1929), who recognized many species in this complex. Even so, it means that

there will remain many specimens that will have to be placed somewhat arbitrarily in one or the other species. Thus, while we have not made the species any "easier" to identify, we have shown some reasons for the taxonomic difficulties inherent in this polyploid complex.

SUMMARY

Twenty-five new artificial hybrids involving polyploid species are reported. The five tetraploid species of the eastern United States have been connected by a series of hybrids. These hybrids are generally fertile and show fairly regular chromosome pairing. A similar situation holds for the five hexaploid taxa of the same area. Several heteroploid hybrids are reported and their chromosome pairing discussed. Four colchicine-induced tetraploid perennials have been obtained which are cytologically similar to the naturally occurring tetraploids. It is concluded that the tetraploid perennials of the eastern United States are either segmental allopolyploids or autopolyploids derived from the eastern perennial diploids. The hexaploids in all probability have two genomes from these tetraploids. Although Kostoff's suggestion that the third genome of the hexaploids comes from a sunflower similar to *Helianthus annuus* cannot yet be ruled out, it appears possible on morphological and geographical grounds that the third genome was supplied by the eastern perennials. In view of the fact that several hybrids have been secured between diploid annuals and perennials which exhibit good pairing, genomic analysis fails to supply critical evidence bearing on the origin of the hexaploids. It is pointed out that the analysis of the hybrids helps explain the complicated taxonomic situation existing in the polyploid species.

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